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Biology and biogeography of the chalk-hill blue *Polyommatus coridon* – insect of the year 2015 for Germany, Austria and Switzerland

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Abstract. The chalk-hill blue was nominated insect of the year 2015 for Germany, Austria and Switzerland. The species is strongly associated with base-rich short-turfed swards; the caterpillars feed mainly on horseshoe vetch *Hippocrepis comosa* and show myrmecophilous behaviour. The species is restricted to Europe, where it is widely distributed but missing from the northern parts of the continent. *Polyommatus coridon* survived the last ice age in Mediterranean refugia in Italy and the Balkan Peninsula from where it colonised more northern regions postglacially.

The chalk-hill blue – insect of the year 2015 for Germany, Austria and Switzerland

The insect of the year for Germany, Austria and Switzerland has been nominated by a curatorium every year since 1999. This panel is composed of experts representing a variety of scientific societies and institutions in these three countries. The goal is to advertise insects in general to a broader public by focusing on one charismatic species every year. However, the aesthetic appeal of the selected species is not the most important aspect of the insect of the year. Beauty in this case is just a vehicle to stimulate interest in the highly remarkable ecology and behaviour of the species. In particular, the nomination of an insect of the year is intended to enhance awareness of the general importance of insects and the necessity of their conservation. After nomination of the brimstone *Gonepteryx rhamni* in 2002 and the burnet *Zygaena carniolica* in 2008, the chalk-hill blue *Polyommatus coridon* (Poda, 1761) (Figure 1) became the third lepidopteran species to be nominated insect of the year, in 2015. Against this background, an overview of the biology and biogeography of this butterfly species is presented.

Portrait of the species

The wing pattern of the chalk-hill blue is remarkably dimorphic. The colour of the upperside of the wings is light blue in the male, often with a silvery hue. The margin of the forewings is brown, but the width of this varies regionally. A pattern of white circles can be observed in this margin. However, this patterning is much less frequent in eastern than in western European populations (Schmitt et al. 2005). On the hindwing, this margin is mostly dissected into brown spots with white margins.

Figure 1. A freshly emerged male of the chalk-hill blue with open wings sitting on the dry inflorescence of a knapweed. Spiazzi, Monte Baldo, northern Italy, 02.IX.2013. Photo: Thomas Schmitt.

The dominating colour of the wing upperside of the females is brown. The hindwings in most cases show orange spots at the margin. These spots are less pronounced on the forewing and fade out towards the apex. The darker central spot on the forewing is often bordered by a narrow white line (Figure 2).

The underside of both wings has a characteristic spot pattern, which is similar in males and females. The dark spots are always surrounded by white lines. The colour of the underside of the wings is always lighter in males than in females. In males this is a slightly yellowish light brown or pale grey, whereas in females it is a considerably darker brown (Figure 3).

The larvae have a typically lycaenid shape. Their dominant colour is greenish, but with a somewhat dirty aspect. Two broken yellow lines run dorsally along the entire body. Other yellow markings can be found laterally (Figure 4).

Closely related species

In central Europe, the male of the chalk-hill blue can hardly be mixed up with any other lycaenid. A somewhat similar blue is only observed in *Polyommatus damon* and *Polyommatus daphnis*, but these two species show considerably different wing patterning (Settele et al. 2009). However, the situation becomes much more complicated in south-western Europe. *Polyommatus hispana* is widely distributed in eastern Spain, southern France and a geographically rather limited area

Figure 2. Copula of the chalk-hill blue with open wings sitting on the inflorescence of a blue-flowering *Eryngium* species. The differences in wing pattern between female (left) and male (right) are easily recognised. Spiazzi, Monte Baldo, northern Italy, 02.IX.2013. Photo: Thomas Schmitt.

in north-western Italy. This sibling species is morphologically mostly similar to *P. coridon*, but allozyme polymorphisms strongly supports it status as a distinct species (Schmitt et al. 2005). Also *Polyommatus albicans*, widely distributed in central Iberia, but also in the Atlas Mountains of Morocco, is difficult to distinguish if relying on its morphology alone; however, the colour of the wings in general is more whitish than in *P. coridon*.

The species status of *Polyommatus philippi*, which is restricted to a limited region in north-eastern Greece, is highly controversial and it has often been synonymised with *P. coridon*. Also the morphologically differing *P. coridon caelestissima*, which is endemic to a restricted area in eastern Spain geographically separated from the continuous distribution of the species, has a doubtful taxonomic status. In this case, the males have a sky-blue and not a light silvery blue wing colour; it is still debated whether this taxon represents a well differentiated subspecies or a separate species (Fernández-Rubio 1991, Tolman and Lewington 1998, Tshikolovets 2011).

The populations in the mountain areas of the islands of Corsica and Sardinia were only discovered in the 1970s and 1980s, respectively, and were described as *P. coridon nufrellensis* and *P. coridon gennargenti*. While the former is mostly accepted as being just a subspecies of *P. coridon*, the latter is frequently assumed to be a good species, as supported for example by genetic analysis and rearing experiments (Marchi et al. 1996, Jutzeler et al. 2003). *Polyommatus corydonius* is

Figure 3. Copula of the chalk-hill blue with closed wings. The differences in wing pattern between female (left) and male (right) are easily recognised. Csákvár, Vértes mountains, western Hungary, 08.VIII.2014. Photo: Thomas Schmitt.

another morphologically similar species distributed in Turkey and the Caucasus region, but which never occurs in sympatry with *P. coridon* (Tshikolovets 2011).

The female of *P. coridon* is much more easily misidentified than the male as it is rather similar to several other species. Even females of *Polyommatus bellargus*, which is well differentiated in males by the sky-blue wing colour, are not easy to distinguish. One of the clearest characters of the female *P. coridon* is the distribution of the intensity of the brown colour on the underside of the forewing: the relatively dark brown at the margins becomes gradually lighter to the centre. However, particularly in old and hence worn females, this cannot be assessed without doubt remaining in some cases (Tolman and Lewington 1998, Tshikolovets 2011).

Due to the close relatedness within the genus *Polyommatus*, natural interspecific hybrids are frequently observed, as for example between *P. coridon* and *P. bellargus* (e.g. de Lesse 1969a). These hybrids have an intermediate pattern and colouring of the wings and are named *Polyommatus* × *polonus*.

Life cycle

The chalk-hill blue is strictly univoltine over most of its range. Males in most regions start emerging by mid-July. A peak of male emergence can often be observed around 20 July. Early males may

Figure 4. The caterpillar of the chalk-hill blue shortly before pupation, on its host plant horse-shoe vetch, being visited by an ant. Photo: Albert Krebs (E-Pics ETH Zürich). Publication with permission of the copyright holders.

occur in the first half of July or even in late June, but are relatively rare (Ebert and Rennwald 1991, Haag and Eller 2007, Trampenau 2007, Pfeuffer 2013); exceptionally early sightings were recorded for Bavaria where butterflies were observed in the wild as early as 15 May (Pfeuffer 2013). Such early males might be predestined for hybridisation with females of the first generation of *P. bellargus*. However, even in rather warm and dry years, the normal flight season of *P. coridon* is only marginally earlier than in normal years. Females mostly emerge one week later than males, hence showing protandry (Thiel and Meyer 2007), as in many other butterflies and insects in general. The flight season of the chalk-hill blue is relatively long, but the number of individuals starts to decline around 20 August in most years. Nevertheless, the species is frequently still to be observed in early September, but mostly in relatively small numbers. Observations in the second half of September have only been made in some years. Sightings in early October exist, but are exceptions.

Truly bivoltine populations are only known in a geographically restricted area of south-western Slovakia in the Vah valley. They were even described as a separate species, *Polyommatus slovacus* (Vít'az et al. 1997). However, analyses of allozyme polymorphisms clearly demonstrated that these bivoltine populations show no genetic differentiation from the nearest univoltine populations; furthermore, no indication of a genetic bottleneck could be detected; therefore, their species status has to be rejected (Schmitt et al. 2005). In these bivoltine populations of south-western Slovakia, a first generation by the end of May and in June composed of relatively small numbers of individuals is followed by a second generation, which normally is much more numerous than the first generation and on the wing during the normal flight period of univoltine populations of adjoining regions (Schmitt et al. 2005).

The closely related *P. hispana* in eastern Spain and southern France (Kudrna et al. 2011) also has two generations a year, but the first one is on the wing earlier than in the Vah valley, while the second one tends to be later than *P. coridon* (Tolman & Lewington, 1998). All other closely related species only have a single generation per year, with adults flying in mid-summer (Tshikolovets 2011).

Populations of *P. coridon* other than that in the Vah valley are strictly univoltine. Schurian (1989) reports that it is not possible to obtain the next generation of butterflies without diapause, albeit under artificial breeding conditions. However, Comont et al. (2009) obtained spontaneous development of British provenances, with adults reared in a green house but under conditions similar to the normal climatic environmental conditions emerging by mid-November. A similar phenomenon also might explain the few exceptionally early butterflies observed in Bavaria (see above).

The females lay their eggs after being fertilised. Often the eggs are not laid directly on the larval host plant, but on dry grass or moss nearby. If eggs are laid directly on the larval host plant, this is not on living parts of the plant like shoots and flowers, but on dry parts (Ebert and Rennwald 1991, Pfeuffer 2000). The young larva, when ready to hatch, remains in the egg shell for the entire winter (but see Comont et al. 2009). It only hatches in the following spring when the sun heats its surroundings to an adequate temperature. Hatching thus takes place from mid-March onwards. The caterpillars then develop relatively quickly, but considerably more slowly than related lycaenid species with more than one generation per year. Pupation takes place close to the ground, close to the host plants, in early June or later. The pupal stage lasts about one month, so that the imagoes hatch punctually by mid-July, thereby completing one complete life cycle (Ebert and Rennwald 1991).

Habitats

The chalk-hill blue has relatively demanding habitat requirements (Brereton et al. 2008). The most typical habitats in central Europe are semi-natural calcareous grasslands such as Mesobrometum (Figure 5) and Xerobrometum, but also the Coelerietum, often in the form of pastured *Juniperus* heathlands (Figure 6) (Ebert and Rennwald 1991, Haag and Eller 2007, Pfeuffer 2013). Additionally, the sparse vegetation which rapidly becomes established in abandoned limestone queries and is often remarkably similar structurally to the above mentioned grasslands can be suitable habitats too (Lotzing 1990, Beneš and Konvička 2002, Höttinger et al. 2013). At some places, as for example in the Nahe valley (Rhineland-Palatinate, Germany) or in northern Bohemia, *P. coridon* is also present on base-rich soils over vulcanitic rocks, especially on rocky slopes with sparse vegetation and on *Stipa* grasslands. Occurrences on acid or neutral soils are really rare in western Europe (e.g. the Rotenfels in the Nahe valley, Rhineland-Palatinate, Germany). Occurrences on such soils are somewhat more common, but still rare, in eastern and south-eastern Europe. This difference might be also due to the regional differences in the level of larval host plant specialisation with western European populations being more specific than eastern ones (see below).

In some regions, in particular in eastern Brandenburg (e.g. on the slopes along the river Oder), large populations are also found on base-rich sandy soils, where the preferred habitats are *Stipa* grasslands. However, occurrences on sandy soils are rather rare elsewhere. One of these exceptions is the Mainzer Sand in Rhineland-Palatinate (Germany).

Large populations of the chalk-hill blue can also be observed in the southern part of the species range. However, here it retreats from the hot plains and valleys and inhabits the somewhat cooler hills and mountains. The karst regions of the Balkan Peninsula (Figure 7) and the Apennines in Italy are regions of southern Europe with a particularly high number of suitable habitats.

Figure 5. The Mesobrometum represents a characteristic habitat of the chalk-hill blue. The photos show a typical habitat in spring when the caterpillars are shortly before pupation. Nature Reserve Perfeist near Wasserliesch (Rhineland-Palatinate, Germany), 10.V.2009. Photos: Thomas Schmitt.

Figure 6. Flower-rich *Juniperus* heathlands, which belong to the plant association Coelerietum, are among the best habitats for the chalk-hill blue. The photos show the summer aspect when the butterflies are on the wing. Bucovica, Durmitor, Montenegro, 31.VII.2014. Photos: Thomas Schmitt.

In calcareous mountain ranges, the butterflies can be found on highly inaccessible rocky slopes (Fig. 8) where they inhabit small patches of grassland on steep slopes and within rocky fields. Here, the imagoes use the existing flowers for nectaring and the larvae feed on their host plants, which can be found between stones. However, the population densities are generally lower in these habitats than they are in the most suitable ones.

Although the chalk-hill blue is considered to be a moderately thermophilic species, individual-rich populations are observed in the Alps as high as 2000 m asl. However, the numbers of individuals decreases considerably above 2000 m asl., with only occasional observations documented from above 2500 m asl. (Schweizerischer Bund für Naturschutz 1987, Huemer 2004, Stettmer et al. 2007). It is remarkable that individuals in the Alps are also found in regions with acidic ground rock where this is intermixed with other more base-rich rock or even limestone. This phenomenon can for example be observed in the Großglockner and the Matterhorn regions.

Figure 7. The karst landscapes in the southern European mountain regions have many habitats suitable for the chalk-hill blue. The habitat here is in the border region of Bulgaria and Greece at an altitude of about 1500 m asl. Trigrad, southern Bulgaria, 04.VIII.2010. Photo: Thomas Schmitt.

Ecology of the larvae

The caterpillars preferably feed on the horse-shoe vetch *Hippocrepis comosa* (Figure 9). This species apparently is the exclusive larval host plant in the western part of the range. In more eastern regions from the Balkan Peninsula in the South to Brandenburg and Poland in the North, the larvae also feed on the purple crown vetch *Securigera varia* (Abb. 10) (Beneš and Konvička 2002, Höttinger et al. 2013). In some regions without populations of horse-shoe vetch, as in Poland, eastern Brandenburg and Saxony, purple crown vetch can even be the only host plant of the caterpillars (Trampenau 2007, Buszko and Masłowski 2008, Settele et al. 2009). Some authors also mention the liquorice milkvetch *Astragalus glycyphyllos* (Schweizerischer Bund für Naturschutz 1987, Höttinger et al. 2013); however, this host plant might be generally of minor importance. Tshikolovets (2011) additionally mentions *Hippocrepis glauca*, a species restricted to the Mediterranean region. For the populations from Corsica, *Hippocrepis conradiae*, endemic to this island, was mentioned as a host plant (Parmentier and Zinszner 2013). Searching for the caterpillars is relatively easy, as they can frequently be found beneath larger individuals of their host plants, often in the moss layer (Ebert and Rennwald 1991).

The caterpillars are often accompanied by ants, with which they live in symbiosis (e.g. Schurian 1989, Ebert and Rennwald 1991, Fiedler et al. 1992, Pfeuffer 2000, Asher et al. 2001). The chalk-hill

Figure 8. The chalk-hill blue is also found on rocky cliffs with limited accessibility. The butterflies use the small grassy habitat patches, which are scattered over the steep slopes. Baile Herculane, Cerna valley, south-western Romania, 29.VII.2010. Photo: Thomas Schmitt.

blue is hence a myrmecophilous butterfly species, as are many lycaenids (Figure 4). Both partners benefit from this association (but see Malicky 1969, 1970 for an alternative opinion). The caterpillars have special glands from which they secret a liquid rich in sugar and amino acids, which is taken up by the ants (Maschwitz et al. 1975, Daniels et al. 2005). Fiedler and Maschwitz (1988) were even able to show that the amount of honeydew-like secret production is sufficiently high to "contribute significantly to the nutrition of the attending ants".

In return, the ants defend "their" caterpillars against enemies. Thus, they hinder for example parasitoids such as parasitic wasps and flies from laying their eggs on the larvae. However, the presence of the ants might also be a general protection against other, more opportunistic, predators. Hence, the carnivorous ants protect an otherwise suitable prey. However, this protection is far from being perfect; many caterpillars of the chalk-hill blue are still infested by parasitoids. Nevertheless, even the pupae are frequently found close to ant nests (Pfeuffer 2000, Asher et al. 2001). This symbiosis has already been observed for different ant species. In central Europe, relationships with *P. coridon* are known to involve the genera *Lasius*, *Tetramorium* and *Myrmica* (e.g. Fiedler 1987, Maschwitz and Fiedler 1988, Schurian 1989, Ebert and Rennwald 1991, Fiedler et al. 1992, Pfeuffer 2000, 2013).

In general, myrmecophilous behaviour has frequently been observed in many lycaenid species, with many ant species involved all around the world (e.g. Fiedler et al. 1991, New 1993). The

Figure 9. The horse-shoe vetch *Hippocrepis comosa* is the most important larval host plant of the chalk-hill blue. In the western part of its distribution, this plant species is even the only host plant. An inflorescence is shown to the left, the typical pinnate leaves to the right. Gánt, Vértes mountains, western Hungary, 21.VII.2014. Photos: Thomas Schmitt.

Figure 10. The purple crown vetch *Securigera varia* is an important additional larval host plant from the Balkan Peninsula to eastern Brandenburg and Poland. In some regions, e.g. Brandenburg, this plant is the sole larval host plant. Strausberg, eastern Brandenburg, 17.VI.2014. Photo: Thomas Schmitt.

protective benefits for the larvae of lycaenids have already been demonstrated in the wild for *Glaucopsyche lygdamus* (Pierce and Mead 1981, Pierce and Easteal 1986). Furthermore, higher growth rates of lycaenid larvae with than without ant attendance have been demonstrated (e.g. Fiedler and Saam 1994, Wagner and del Rio 1997).

Ecology of the imagoes

The butterflies are much less choosy in the selection of their nectar sources than the caterpillars are with their host plants. However, the imagoes tend to prefer classic butterfly flowers, mostly of the plant families Lamiaceae, Asteraceae and Caprifoliaceae, although species of Leguminosae are also frequently visited for nectaring. The most visited plant genera are apparently *Origanum*, *Scabiosa*, *Knautia* and *Centaurea* (Weidemann 1986, Ebert and Rennwald 1991, Lörtscher et al. 1995, Pfeuffer 2013). The distribution of nectar sources strongly influences the microdistribution of the butterflies within the habitat (Lörtscher et al. 1995). It seems that butterflies give preference to violet flower heads, but visits to white and yellow flowers can also frequently be observed (Fig. 11). However, the butterflies also gather at muddy places to take up water (e.g. Pfeuffer 2013) and even visit excrements and carcasses (e.g. Jones 2000). Like many other lycaenids, the chalk-hill blue aggregates in sleeping groups in the evening (Figure 12) (e.g. Weidemann 1986). After sunset, they mostly descend into the more closed vegetation to spend the night.

On sunny days, it is mainly the male individuals that can be observed flying around in the habitat. Females fly less and invest more time in nectaring or just sitting in the vegetation. Therefore, one might get the impression that fewer females than males are present. However, this impression is misleading. Rearing of more than a hundred larvae randomly collected in the wild in Olk (southern Eifel, Rhineland-Palatinate, Germany) resulted in a nearly equal number of both sexes (Ashoff and Schmitt 2014).

The intensive flight activity within habitats leads one intuitively to overestimate the actual distance of translocations within and between habitats. Thus, a mark-release-recapture experiment with 2,211 marked butterflies in the Keuperscharren area south-west of Bitburg (southern Eifel, Rhineland-Palatinate, Germany) demonstrated that the exchange between habitat patches is much less than one would expect from the high flight activity of the butterflies. Only four individuals were detected to have moved between two patches separated by a distance of 600 m containing arable fields and intensive grassland with few flowers. Just one butterfly was found to have travelled a greater distance of 3.7 km (Schmitt et al. 2006). Similar experiments in Hampshire (southern Britain) showed that only 1 to 2% of the population exchanged between populations one to two km apart (Asher 2001). In another study in southern Britain, only 12 out of 1,797 marked butterflies moved between the three analysed habitats which were 350 to 1100 m distant from each other; however, five individuals even crossed a motorway while changing their habitat (Adey and Wilson 2010). In Luxembourg, none of 304 recaptured individuals (out of 2,085 marked ones) moved between three sites that were 4.2 to 11.2 km apart from each other (Thiel and Meyer 2007). For *P. gennargenti*, which might or might not be conspecific with *P. coridon* (see above), mark-release-recapture in four habitat patches with a maximum distance of 350 m between them showed that, with the exception of one rather small patch, emigration rates ranged from 3 to 11% (Casula et al. 2004).

In Britain, however, *P. coridon* adults were also found 10 to 20 km from known colonies, thus supporting the idea that a rather small (but ecologically highly important) proportion of the individ-

Figure 11. The imagoes of the chalk-hill blue visit flowers of different plant species for nectaring, here the cream scabious *Scabiosa ocholeuca* (left: Csákvár, Vértes mountains, western Hungary, 21.VII.2014) and a yellow-flowering Fabaceae (right: Luka nad Vahom, south-western Slovakia, 09.VIII.2014; note that the depicted individual is a member of the second generation of a bivoltine population). Photos: Thomas Schmitt.

uals is quite mobile (Asher et al. 2001). Similar findings are also known for Baden-Württemberg (Ebert and Rennwald 1991). One such particular case is described in more detail by Leverton (2014).

Even within a seemingly homogeneous habitat, the individuals did not mix randomly. Thus in the study performed in the Keuperscharren near Bitburg, one of the patches with a size of 6.7 ha was divided into two parts similar in size. No discontinuity in habitat separated these two subplots. Only 15 individuals out of 703 marked here could be recaptured. However, 13 of these were recaptured in the sector where they were first marked, and only two changed over to the respective other subplot (Schmitt et al. 2006). A quite similar finding was made in Luxembourg where only 12.5% of the recaptured individuals within one major calcareous grassland area were detected on a different part of this habitat (Thiel and Meyer 2007). This clearly demonstrates that individuals living in a larger habitat plot only use a relatively small fraction of the available habitat for their daily activities. Lörtscher et al. (1997) also supported this point of view by demonstrating in their mark-release-recapture experiment in Alpe di Poma (Ticino, Switzerland) that males on average moved 135 m between two capture events and did not mix randomly within one habitat. This was even more pronounced in females, which moved significantly less (on average 90 m) than males and changed between different parts of the habitat less frequently.

Further unpublished studies by the author in the nature reserve Badstube near Mimbach (Bliesgau, Saarland, Germany) in the year 1998 also support these data. The results of this study, based on more than 3,000 marked individuals, also showed that no random mixing took place on a seemingly homogeneous grassland area of some few hectares. Furthermore, a strip of deciduous forest within a deeply incised valley of approximately 100 m width reduced exchange to some very few individuals. However, it seems to be a common behavioural pattern of butterflies not to use larger continuous habitats entirely, but only a fraction of these, even if they do not exhibit territorial behaviour. A further example of this phenomenon is the lesser marbled fritillary *Brenthis ino*, studied in an assay in which all individuals were marked individually and positioned by a GPS device (Weyer and Schmitt 2013).

Despite these low exchange rates among habitats, mobility in general seems to be sufficient to counteract noticeable differentiation among populations, as was demonstrated by genetic analyses;

Figure 12. The imagoes of the chalk-hill blue often congregate in sleeping groups in the evening. Many individuals can assemble at exposed places, to utilise the last sunshine of the day. Gánt, Vértes mountains, western Hungary, 08.VIII.2014. Photo: Thomas Schmitt.

also see the rare long distance movements cited above (Ebert and Rennwald 1991, Asher et al. 2001). One study of allozyme polymorphisms at 20 different loci included 874 individuals from 22 populations sampled in Rhineland-Palatinate and the Saarland. The Bliesgau, a region with a remarkable density of viable populations (Schmitt 2002), had no significant genetic differentiation between the analysed populations. The amount of exchange in this region seems to be sufficient to completely hinder genetic differentiation between these populations. The calcareous regions of the western Saarland, the southern Eifel and the central Eifel, which all have a less dense network of populations than the Bliesgau, also had low rates of genetic differentiation among populations, and the mean of genetic variance between populations was less than 2% of the entire variance in all three of them. Hence, genetic differentiation between populations is apparently far from being critical in terms of conservation. The limited exchange rates seem to be sufficient to bolster against such a differentiation. Nevertheless, the larger populations expressed higher genetic diversity than the small ones (Schmitt and Seitz 2002a). Similar genetic findings with low differentiation between populations are also known for the Göttingen region. Here, it was demonstrated that the Leine valley with its intensive agriculture genetically separated the populations to the East and West of it (Krauss et al. 2004).

These results on population genetics are mostly supported by a classical ecological study from the Göttingen region which demonstrated that the population density of *P. coridon* is mainly dependent on the quantity of its larval host plant, in this case *H. comosa*, but not on the effect of habitat isolation and habitat quality (Krauss et al. 2005). Quite similar results were obtained by Rosin et al. (2011) southwest of Kraków (southern Poland); they showed that the best predictors for a potential habitat being occupied or not are its size and the percentage cover by the host plant, in this case *S. varia*. Hence, the chalk-hill blue is mostly dependent on the preservation of large habitats.

Another study from the Göttingen area yielded somewhat different results. No impact of the habitat area on the butterfly was found, but the importance of habitat connectivity was revealed. However, connectivity neither impacted the larval host plant occurrence nor the infection rate by parasitoids (Brückmann et al. 2011). This is also supported by population genetic data from this region showing that the expected heterozygosity of allozymes decreased with distance to other populations (Krauss et al. 2004).

Distribution and biogeography

The chalk-hill blue is mostly restricted to Europe (Kudrna et al. 2011), and the species is only found in a very restricted part of western Asia north of the Caspian Sea (Anikin et al. 1993, Lukhtanov and Lukhtanov 1994); it is missing in Turkey apart from a record of a single individual (Hesselbarth et al. 1995). The border of its south-western distribution is located in northern Spain (García-Barros et al. 2004). In the North-West, *P. coridon* is found up to south-eastern England (Emmet and Heath 1990; Asher et al. 2001). In Italy, the species can be found throughout the peninsula, but mostly in the Apennines at higher altitudes. Similarly, the species is widespread in the Balkan Peninsula where it is found as far south as the Peloponnese, but predominantly in mountain ranges (Pamperis 1997). The northern limit of distribution stretches along the northern margin of the German middle mountains (Bink 1992), and in the Netherlands it is only found in the extreme South of the country (Wynhoff et al. 1992). In eastern Germany, the chalk-hill blue is found along the Oder almost as far north as the Baltic Sea, which is reached in Poland (Buszko 1997, Buszko and Masłowski 2008). The species is completely missing in Scandinavia (Henriksen and Kreutzer 1982).

Studies of allozyme polymorphisms of several thousands of individuals of the chalk-hill blue allowed the reconstruction of the distribution dynamics over time. In this context, two major genetic lineages could be distinguished. A western lineage is found in Italy, France, the western and central Alps and major parts of Germany. An eastern lineage is distributed from the Balkan Peninsula, stretching over the Carpathian Basin to Brandenburg and Poland (Schmitt and Seitz 2001). Sequencing of mitochondrial genes also supports the differentiation into at least two major lineages, an eastern and a western one (Talavera et al. 2013). De Lesse (1969b) distinguished two major groups by their number of chromosomes, a western group with 87 or 88 chromosomes and an eastern group with 90 to 92 chromosomes. The distribution of these two groups almost perfectly matches the distribution of the two major allozyme groups, which also can be distinguished by morphological features (see above). Furthermore, it is only the eastern lineage which commonly uses *S. varia* as its larval host plant.

Along the contact zone between the lineages, intensive hybridisation was detected in some regions of the eastern Alps based on the allozyme data set. However, hybrid populations are rather rare north of the Alps, but for example were also found at two localities in Sachsen-Anhalt (Schmitt and Zimmermann 2012).

Within the western lineage, populations from the Pyrenees are well distinguished from all others. Furthermore, the populations from southern Germany (Baden-Württemberg to southern Thuringia) showed a genetic make-up that distinguished them as an individual group from all other populations (Schmitt et al. 2002). However, this group also includes populations from the Alps, as indicated by still unpublished data. Remarkable differences in genetic diversity can be observed between neighbouring regions in the western lineage, as for example between north-eastern France and western Germany (Schmitt et al. 2002). A continuous loss of genetic diversity from western Hungary to Brandenburg was observed for the eastern lineage. After performing a linear regression for the number of allozyme alleles for these populations, a highly significant correlation ($p < 0.001$) was obtained which explained 78% of the regional variation (Schmitt and Seitz 2002b).

These genetic patterns strongly support the existence of ice age refugia in Italy and in the Balkan Peninsula at least during the last glacial period. Here, these lineages evolved in allopatry. However, the process of evolution was not necessarily restricted to a single glacial period, but might have taken place during repeated periods of glacial isolation in these refugia. Ice age survival in these Mediterranean refugia has long been postulated (de Lattin 1949) and has been supported by numerous phylogeographic analyses since then (cf. Schmitt 2007). However, the differentiation of the populations in the Pyrenees as well as in southern Germany and parts of the Alps calls for additional refuge areas not resembling the pattern of the classical Mediterranean refuge areas. Additional glacial refugia therefore could have existed south of the Pyrenees and Alps. This assumption is also supported by still unpublished data based on sequences of two mitochondrial loci. Hence, the chalk-hill blue shows biogeographical traits of a species that is much more cold-tolerant than previously thought and which was thus able, at least additionally, to survive glacial periods in so called extra-Mediterranean refugia north of the classical Mediterranean refugia (cf. Schmitt and Varga 2012).

These genetic analyses also allow a relatively detailed reconstruction of the postglacial range expansion. The Adriato-Mediterranean lineage evolving in the Italian peninsula most probably had a north-western distribution limit during the last ice age located in north-western Italy or south-eastern France. Starting here, this lineage could colonise the regions northwards to Lorraine without genetic erosion, with the Rhône valley most probably representing an important expansion corridor. During the subsequent expansion into the western German region, remarkable genetic impoverishment has taken place. This might be explained by the, if compared to north-eastern France, considerably less favourable environmental conditions for this species in western Germany resulting in remarkable genetic erosions in the wake of the colonisation of this region (Schmitt et al. 2002).

During glacial conditions, the Ponto-Mediterranean lineage which survived the last ice age in the Balkan Peninsula most probably had its north-western distribution edge in the region of the northern Dalmatian Coast. Starting there, postglacial range expansion reached as far north as eastern Brandenburg. During a first advance, the species was able to colonise to the forelands of the eastern Alps. Here, the route of further expansion bifurcated. An eastern branch ran along the Hungarian middle mountains to eastern Slovakia. A western branch reached Moravia via the Porta Hungarica (lowland area between the north-eastern Alps and the south-western foothills of the Tatra Mountains). By a westwards advance, the species colonised the limestone regions of the Czech Republic. This advance was stopped by the mountain ranges between the Czech Republic and Germany, which were too cold and where soils were too acid to permit the survival of the species; on the other side of these mountains, all populations derive from the Adriato-Mediterranean

region (Schmitt and Zimmermann 2012). The further expansion out of Moravia northwards most probably first followed the river Vistula, and then in a westerly direction along the Torun-Eberswald glacial valley finally reaching eastern Brandenburg; most parts of the Odra region in Poland have rather few suitable habitats available for *P. coridon* so that this putative expansion corridor has to be considered less likely. The linear decline of the number of alleles from western Hungary to eastern Brandenburg implies a constant loss of genetic diversity in the Ponto-Mediterranean lineage during its postglacial range expansion (Schmitt and Seitz 2002b).

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